Fossil Bats (Mammalia: Chiroptera) from the Late Pleistocene and Holocene Vero Fauna, Indian River County, Florida

GARY S. MORGAN
Florida State Museum,
University of Florida, Gainesville, Florida 32611

ABSTRACT.— Six species of bats are reported from the late Pleistocene and Holocene Vero fossil vertebrate locality on the east coast of peninsular Florida: *Eptesicus fuscus*, *Lasiurus intermedius*, *L.* cf. *seminolus*, *Nycticeius humeralis*, *Tadarida brasiliensis*, and *Eumops glaucinus*. This is the first known fossil occurrence of *Lasiurus seminolus*, and the first record of *Nycticeius humeralis* from the Pleistocene of Florida. Previous reports of *Myotis austroriparius* from Vero are shown to be in error, as they were based on a misidentified humerus. The bats from Vero represent the most diverse fossil chiropteran fauna yet known from Florida and one of the richest in the North American Quaternary. This site is unique among Florida fossil vertebrate localities as it samples species of bats that roost primarily in trees, rather than cave-dwelling forms. The six species present at Vero constitute the entire native chiropteran fauna of present-day South Florida, indicating that the bat fauna of this region has remained relatively stable over the past 10,000 years.

INTRODUCTION

Recent curation of the abundant microvertebrate fossils collected by Robert D. Weigel in 1956 and 1957, during his re-excavation of the classic Vero Site on the Atlantic coast of Florida (Weigel 1962), revealed the presence of a relatively large sample of bat remains. Based on only four elements, Weigel (1962) recognized three genera of bats from Vero—*Myotis*, *Eptesicus*, and *Lasiurus*. He did not assign any of his material to species, and his identification of *Myotis* was incorrect. Detailed study of the bat fossils from Vero, especially the postcranial elements, and a re-examination of the small sample identified by Weigel, allows for more precise identification of most of the material. In the present study, six species of bats are recognized from the Vero deposits based on 37 elements representing 16 individuals. Comparison with data in Webb (1974:14, Table 2.1) indicates that the six species of bats at Vero make it the most diverse fossil bat fauna yet known from Florida.

DESCRIPTION OF LOCALITY

The Vero fauna is one of the best known late Pleistocene (Rancholabrean) local faunas in Florida (see Weigel 1962 for a complete list of

fossil vertebrates from Vero). Vero engendered considerable controversy in the early part of this century, as it was the first fossil site in the New World where human bones and artifacts were supposedly found in association with extinct Pleistocene vertebrates. The site was discovered in November 1913 during excavation of an east-west drainage canal through the town of Vero Beach by the Indian River Farms Company. Between 1913 and 1917, Isaac M. Weills and Frank Ayers collected the majority of the vertebrate fossils and human remains that formed the basis for a large number of publications on the site (see Ray 1957 and Weigel 1962 for a complete bibliography). The fossil site is located within the present city limits of Vero Beach, Indian River County, Florida (center of SE1/4, sec. 35, T32S, R39E, Vero Beach Quadrangle, USGS 7.5 min. series; 27°39'N latitude, 80°24'W longitude), southeast of the Vero Beach airport and immediately south of the Florida East Coast Railroad. The paleontological and historical significance of Vero, coupled with the paucity of microvertebrate fossils in the early collections, prompted Weigel to conduct extensive field work at the site during the summers of 1956 and 1957.

The fossil-bearing deposits at Vero consist of three distinct units, designated from bottom to top as Strata 1, 2, and 3 by Sellards (1917) and all later workers except Weigel (1962). He called them Beds 1, 2, and 3. According to Weigel, the three strata are easily recognized throughout the site and fill a shallow sedimentary basin approximately 100 m in diameter. A typical stratigraphic section at Vero and a map of his various excavations within the site can be found in Weigel (1962). The total thickness of strata at Vero does not exceed 3 m, of which only 1.5 to 2 m constitute the bone-bearing Strata 2 and 3. Stratum 1 is a late Pleistocene marine shell marl referred to the Anastasia Formation by Sellards (1916) that has produced no terrestrial or freshwater vertebrate fossils. Lying above the Anastasia Formation and separated from it by an erosional unconformity is Statum 2, consisting of white beach sands at the base, grading upward into coarse and fine brown stained sands that become darker toward the top of the bed. The vertebrate fossils from Stratum 2 are heavily permineralized and include 17 species of extinct Pleistocene megafauna. The contact between Strata 2 and 3 is horizontal, and is sharply demarcated by the contrast between the relatively dark brown upper portion of Stratum 2 and the relatively light colored sands of Stratum 3. Stratum 3 consists of loose white sands, muck, and peat, banded with decayed plant material. Bones from this layer are extremely abundant, stained very dark brown, and are barely permineralized. In his excavations, Weigel found no remains of extinct vertebrates in Stratum 3, except at his Locality 1, which corresponds with the area where much of the early fossil material was collected by

Weills and Ayers. According to Weigel, the beds appeared to be disturbed at Locality 1. A small creek flowed through this locality, apparently cutting through Strata 2 and 3 and mixing fossils from these beds with more recent artifacts and human bone. In six other stratigraphic sections at Vero, Weigel found no extinct vertebrates in Stratum 3 and no evidence of stream channel fills or other reworked deposits.

Owing to the presence of human remains at Vero, the age of the various strata there has raised much controversy. Weigel (1962:8-9) gave five radiocarbon dates for Stratum 2, ranging in age from 3,550 years before present (ybp) to greater than 30,000 ybp. Based on a radiocarbon date from the top of Stratum 2, Weigel (1962) hypothesized that now extinct vertebrates may have persisted in Florida until 3,500 years ago. In retrospect, it appears clear that this date is erroneous, as recent studies based on extensive series of radiocarbon dates (Meltzer and Mead 1983) suggest that no members of the extinct Pleistocene megafauna survived in North America beyond 10,000 ybp. Although no radiocarbon dates are available from Stratum 3, the absence of extinct Pleistocene megafauna and the predominance of species found in the immediate vicinity at the present time, indicate that this part of the fauna is Holocene in age. Holocene faunas are uncommon in Florida, or at least they have rarely been recognized and studied. The late Pleistocene and early Holocene Devil's Den fauna (Martin and Webb 1974), and the Nichol's Hammock fauna (Hirschfeld 1968) of unknown but probably late Holocene age, are the best known. In this paper, vertebrate fossils from Stratum 2 are regarded as late Wisconsinan (late Pleistocene, Rancholabrean), while fossils from Stratum 3, in particular the extremely rich microvertebrate sample from Weigel's Site 3a, are considered Holocene. Only four bat fossils were recovered from Stratum 2 in Weigel's excavations, the mandible he referred to *Eptesicus* sp. and three specimens of *Nycticeius humeralis*. All six species identified from Vero are present in Stratum 3, where the great majority of the bat remains occur.

METHODS AND MATERIALS

Skulls and postcranial skeletons of all 11 species of Recent bats native to Florida were available for comparison with the fossil material from Vero. Where possible, specimens from localities in southern Florida were used for comparisons. Only one maxillary fragment is present among the Vero chiropteran fossils, while mandibles are slightly more common. The most important mandibular characters used in differentiating the various species were overall size, number and form of the premolars, morphology of the molars, length of the ramus, shape of the coronoid process, and development of the masseteric fossa. Very few previous studies of bats from Florida Pleistocene localities have included

postcranial material, even though limb elements are often quite abundant in sites where bat fossils occur. In fact, two of the bat species identified from Vero are based only on postcranial material. The classic study of Miller (1907) used characters of the humerus, in addition to more conventional cranial and dental characters, to diagnose many of the higher taxonomic groups of bats. In her work on the fossil bats from the Miocene Thomas Farm Site in northern Florida, Lawrence (1943) discussed the taxonomic importance of the humerus in bats, demonstrating that almost all Recent genera of North American vespertilionids could be distinguished using characters of the proximal and distal ends of the humerus. The radius, especially the proximal end, is useful in distinguishing between certain groups of bats, although it lacks the large number of diagnostic characters found in the humerus. Terminology for various structures on the humerus and proximal end of the radius follows Vaughan (1959) and Smith (1972). Miller (1907) and Lawrence (1943) used the terms trochiter and trochin for the greater and lesser tuberosity of the humerus, respectively. However, since these structures are homologous with the greater and lesser tuberosity of other mammals, the latter terms will be used in this paper. Dental terminology is standard for mammals (Szalay 1969). Site names followed by Roman numerals refer to fossil sites listed in the Florida State Museum vertebrate paleontology locality files. Cranial and dental measurements were taken with a Gaertner measuring microscope accurate to 0.01 mm. Postcranial measurements were taken with dial calipers accurate to 0.10 mm.

All recent comparative material is from the Mammal Collection of the Florida State Museum, University of Florida (UF). The Vero fossils are from the Florida Geological Survey Collection, formerly housed in Tallahassee and now merged with the Florida State Museum Fossil Vertebrate Collection in Gainesville (UF/FGS, catalogue number preceded by V).

SYSTEMATIC PALEONTOLOGY

Order Chiroptera Blumenbach

Family Vespertilionidae Gray

Eptesicus fuscus (Palisot de Beauvois, 1796)

Referred material.—Stratum 2-V7200, partial left mandible with m_3; Stratum unknown-V7201, complete edentulous left mandible.

Recent distribution.—*Eptesicus fuscus* is one of the most widespread bats in the New World. It occurs throughout the United States, southern Canada, Greater Antilles, Bahamas, Middle America, and northern South America. In Florida, the big brown bat has been

recorded as far south as Englewood in southern Sarasota County on the west coast and from southern Highlands County in the central portion of the peninsula.

Fossil record.—Vero is the only Pleistocene fauna in Florida from which *Eptesicus fuscus* has been reported (listed as *Eptesicus* sp. by Webb 1974 and Weigel 1962). I have recently identified *E. fuscus* in two additional late Pleistocene (Rancholabrean) faunas from Florida: Arredondo IIA, Alachua County, and Monkey Jungle Hammock, Dade County. *Eptesicus fuscus* is the most widespread Pleistocene bat in North America, having been reported from more than 25 Rancholabrean faunas, ranging from Pennsylvania and Florida in the east to Wyoming and New Mexico in the west, and as far south as Nuevo Leon, Mexico (Martin 1972). This species has also been reported from a number of late Pleistocene and Holocene cave deposits in the West Indies.

Description and comparisons.—Based on their large size, the two mandibles here referred to *Eptesicus fuscus* can be distinguished from all other Florida bats except *Eumops* and *Lasiurus intermedius*. The mandible of *Eumops* differs in its larger size, reduced coronoid process, and shallow masseteric fossa. *Lasiurus intermedius* can be separated from the fossils by its shorter, more robust mandibular ramus, vertical mandibular symphysis, smaller triangular coronoid process, shallower masseteric fossa lacking a strong anterior ridge, and the more reduced m_3. The two mandibles are readily identified as *E. fuscus* by the long and relatively slender mandibular ramus, high rounded coronoid process, and deep masseteric fossa with a strong anterior ridge. Measurements of the two fossil mandibles compare closely with measurements of recent *E. fuscus* from Florida (Table 1).

Discussion.—Although single specimens of *Eptesicus fuscus* have been collected from a number of localities in the northern two-thirds of Florida, it is considered rare in the state. Likewise, *E. fuscus* is uncommon as a fossil in Florida, having been recorded from only three late Pleistocene sites based on a small handful of specimens. Most recent individuals of *E. fuscus* from Florida have been found in buildings, in association with colonies of *Tadarida brasiliensis*. According to Jennings (1958), the absence of *E. fuscus* from Florida caves is due to the high humidity and damp walls characteristic of these caves. *Eptesicus fuscus* also roosts in hollow trees and rock crevices, the former probably serving as the preferred roosting site in Florida before the appearance of man-made structures. A minimum of two individuals of *E. fuscus* is represented in the Vero deposit based on the presence of two left mandibles. The mandible from Stratum 2 represents one of the few late Pleistocene bat fossils from Vero and was the basis for Weigel's (1962:32) identification of *Eptesicus* sp. from the site.

Table 1. Comparison of mandibular measurements (in mm) of fossil bats from Vero with Recent Florida bats.[1]

	total length of mandible	alveolar length of mandibular tooth row	depth of ramus below m_2	height of coronoid process	length of m_2	width of m_2	length of m_3	width of m_3
Eptesicus fuscus								
Recent	14.5 ± 0.3 3	7.8 ± 0.1 3	2.4 ± 0.1 3	5.4 ± 0.2 3			1.7 ± 0.1 3	1.1 ± 0.1 3
	(14.1-14.7)	(7.8-7.9)	(2.3-2.4)	(5.2-5.6)			(1.6-1.8)	(1.0-1.3)
Fossil								
V7200			2.4				1.8	1.0
V7201	14.5	7.9	2.4	5.6				
Nycticeius humeralis								
Recent	10.7 ± 0.3 10	5.6 ± 0.2 10	1.6 ± 0.1 10		1.3 ± 0.1 10	0.9 ± 0.1 10	1.2 ± 0.1 10	0.8 ± 0.1 10
	(10.2-11.1)	(5.2-5.8)	(1.5-1.7)		(1.3-1.4)	(0.8-1.0)	(1.2-1.3)	(0.7-0.8)
Fossil								
V7228	10.6	5.6	1.7		1.3	0.9	1.2	0.8
Tadarida brasiliensis								
Recent	11.9 ± 0.4 10	6.6 ± 0.1 10	1.6 ± 0.1 10	3.5 ± 0.1 10	1.6 ± 0.1 10	1.2 ± 0.1 10	1.4 ± 0.1 10	1.0 ± 0.1 10
	(11.2-12.6)	(6.4-6.9)	(1.5-1.7)	(3.2-3.7)	(1.5-1.7)	(1.1-1.2)	(1.4-1.5)	(0.9-1.0)
Fossil								
V7218	11.8	6.6	1.7	3.3	1.6	1.2	1.5	0.9

[1] Mean, standard deviation, sample size, and observed range (in parentheses), respectively, are given for Recent specimens.

Lasiurus intermedius H. Allen, 1862

Referred material.—Stratum 3-V7202, proximal two-thirds of left humerus; V7203, proximal end of right radius.

Recent distribution.—*Lasiurus intermedius* occurs primarily in the southeastern United States, from South Carolina to Texas, and into lowland tropical Middle America as far south as Honduras. The yellow bat is found throughout Florida, with records from as far south as Lee County on the west coast and Palm Beach, Broward, and Dade counties on the Atlantic coast (Layne 1974).

Fossil record.—*Lasiurus intermedius* is known as a fossil only from Florida. Webb (1974) recorded this species from three late Pleistocene sites in the state: Haile XIB, Alachua County; Devil's Den, Levy County; and Reddick IA, Marion County. Martin (1972) also identified *L. intermedius* from Arredondo IIA. I have recently identified a mandible of this species from the Glyptodont Site in Pinellas County.

Description and comparisons.—Based on its large size, the humerus referred to *Lasiurus intermedius* can readily be distinguished from all other Florida bats except *Eumops* and *Eptesicus*. The proximal end of the humerus differs from that of *Eptesicus* by the elliptical humeral head oriented at a 45° angle to the shaft, the more prominent greater tuberosity, and the smaller lesser turberosity. It is also readily separable from the humerus of *Eumops* by its smaller size, almost perfectly elliptical head, relatively longer and less expanded pectoral ridge, and lack of a deep groove on the lateral surface of the greater tuberosity. The fossil is identical in size and morphology to humeri of recent *L. intermedius* from Florida (see measurements in Table 2). Although the other large North American species of *Lasiurus*, *L. cinereus*, has been recorded from Florida on several occasions, it occurs there only as a rare migrant. The humerus of *L. cinereus* is larger than the fossil from Vero, with a broader proximal end and relatively thicker shaft.

As with the humerus, the proximal radius referred to *Lasiurus intermedius* needs comparison only with *Eumops* and *Eptesicus*. It is completely unlike the radius of *Eptesicus*, differing from that genus in the more robust shaft, considerably shorter ridge extending distally from the flexor fossa, lack of a deep groove in the articular surface for the capitulum of the humerus, and the acutely triangular shape of the proximalmost extension. The fossil radius can be distinguished from *Eumops* by its smaller size, more laterally placed flexor fossa, more slender shaft, relatively smaller articular surface that is rounded in outline rather than distinctly triangular, and lack of a deep central groove on the articular surface. Although essentially identical to the radius of *Lasiurus cinereus*, the fossil is somewhat smaller, as is the radius of *L. intermedius*.

Discussion.—*Lasiurus intermedius* roosts almost exclusively in trees and appears to be closely associated with Spanish moss (Barbour and Davis 1969). Although the yellow bat is known from more fossil sites (six) in Florida than any other bat species except *Myotis austroriparius*, it is uncommon in the sites where it occurs, generally being represented by only one or two specimens. The rarity of *L. intermedius* remains in fossil sites is not difficult to explain, because the majority of fossil chiropteran faunas in Florida are derived from deposits formed in caves, fissures, or sinkholes. Yellow bats are not known to enter caves, so apparently their presence in cave fossil deposits results from being brought into caves by predators, most likely the Barn Owl, *Tyto alba*. According to Jennings (1958), *L. intermedius* commonly feeds over water, thus providing a possible explanation for the presence of the species at Vero, based on Weigel's (1962) interpretation of the site as a pond or marsh. The two elements of *L. intermedius* identified from Stratum 3 represent one individual.

Lasiurus cf. *seminolus* (Rhoads, 1895)

Referred material.—Stratum 3-V7204, nearly complete right humerus; V7205-7206, proximal ends of right humeri; V7207, distal end of left humerus.

Recent distribution.—*Lasiurus seminolus* occurs primarily in the southeastern United States from North Carolina to Texas. The Seminole bat is found throughout most of Florida, as far south as Lee County on the Gulf Coast and Broward and Dade counties on the east coast.

Fossil record.—This is the first fossil record of *Lasiurus seminolus*, assuming the identification is correct. In general, the small species of *Lasiurus* have a poor fossil record. *Lasiurus borealis* has been reported from only five fossil sites: Reddick IA, Florida (although this could just as easily represent *L. seminolus*); Bat Cave, Missouri; Natural Chimneys and Clark's Cave, Virginia; and Organ-Hedricks Cave, West Virginia (Kurtén and Anderson 1980).

Description and comparisons.—The proximal humeri referred to *Lasiurus* cf. *seminolus* are readily distinguished from all Florida vespertilionids, except *Lasiurus*, by the elliptical humeral head oriented at a 45° angle to the shaft. They can be separated from the proximal humerus of *Tadarida brasiliensis*, the only similar-sized molossid in Florida, by the relatively smaller humeral head, reduced greater and lesser tuberosities, and less expanded pectoral and medial ridges. The single distal humerus agrees with *Lasiurus* and differs from all other Florida bats in the presence of a deeply excavated olecranon fossa. In addition, the fossil and *Lasiurus* can be separated from other Florida vespertilionids by the prominent distal spinous process. Unlike *Tadarida* and most other molossids in which the spinous process is free, the spinous process

Table 2. Comparison of measurements (in mm) of the humerus of fossil bats from Vero with Recent Florida bats.[1]

	total length	proximal width	thickness of shaft	width of distal articular surface
Lasiurus intermedius				
Recent		4.1 ± 0.1 13 (3.9-4.3)	1.6 ± 0.1 11 (1.4-1.8)	
Fossil				
V7202		4.1	1.7	
Lasiurus cinereus				
Recent		4.7 3 (4.6-4.8)	1.8 1	
Lasiurus seminolus				
Recent	26.8 ± 1.4 10 (24.4-28.9)	3.2 ± 0.2 16 (2.9-3.5)	1.4 ± 0.1 16 (1.2-1.6)	2.4 ± 0.1 10 (2.3-2.6)
Lasiurus cf. *seminolus*				
Fossil				
V7204	24.7		1.2	
V7205		3.1	1.4	
V7206		3.0		
V7207				2.3
Lasiurus borealis				
Recent	26.9 ± 0.9 6 (25.8-28.5)	3.3 ± 0.1 13 (3.1-3.4)	1.4 ± 0.1 10 (1.2-1.5)	2.4 ± 0.1 6 (2.3-2.4)
Nycticeius humeralis				
Recent	20.9 ± 0.9 5 (19.8-22.2)	2.9 ± 0.1 18 (2.8-3.1)	1.1 ± 0.1 17 (1.1-1.3)	2.1 ± 0.1 4 (1.9-2.2)
Fossil	20.9 2 (20.3-21.5)	3.0 ± 0.1 7 (2.8-3.2)	1.2 ± 0.1 8 (1.1-1.3)	2.3 ± 0 4 2.3

[1] Mean, standard deviation, sample size, and observed range (in parentheses), respectively, are given for Recent specimens and fossils of *Nycticeius humeralis*.

in *Lasiurus* is attached to the distal articular surface for most of its length.

The humeri referred to *L.* cf. *seminolus* are much smaller than the corresponding element in *L. intermedius* and *L. cinereus*. There are two smaller species of *Lasiurus* known from Florida, *L. seminolus* and *L. borealis*, that have humeri within the size range of the fossils. The

humeri of these two species are broadly overlapping in size (see measurements, Table 2). Examination of a series of humeri of Recent *L. borealis* and *L. seminolus* from Alachua County, Florida revealed no reliable morphological characters that would distinguish them. These species are also very similar in external and cranial morphology. They can, however, be separated by pelage color and the presence of a lachrymal ridge in *L. borealis*. Unfortunately, fossils cannot be definitely assigned to one species or the other without a skull.

Lasiurus borealis occurs primarily in the northern half of the Florida peninsula, having been recorded as far south as Hardee County, although it is not common south of Pasco County. *Lasiurus seminolus* occurs sympatrically with *L. borealis* throughout most of north Florida; however, the Seminole bat is more widely distributed in the southern half of the peninsula and is the only small *Lasiurus* presently found on the east coast of Florida as far south as Indian River County. Because the mammalian fauna from Stratum 3 at Vero closely approximates the Recent fauna of that vicinity, these fossils are tentatively referred to *L. seminolus*.

Discussion.—Like *L. intermedius*, *L. seminolus* roosts primarily in clumps of Spanish moss hanging from trees. Although *L. borealis* is not necessarily associated with Spanish moss, it too roosts almost exclusively in trees. The tree-roosting habits of these two small species undoubtedly account for their rarity in the fossil record. The occurrence of *L. borealis* or *L. seminolus* in the Reddick site is probably a result of Barn Owl predation, while the presence of *L. seminolus* at Vero is most likely related to their preference for feeding near water. Although only four fossils referable to *L. seminolus* were identified from Vero, three of these were proximal ends of right humeri representing a minimum of three individuals.

The proximal half of a right humerus (V7205), identified as *Myotis* sp. by Weigel (1962:32) and later referred to *M. austroriparius* by Webb (1974:14), is actually referable to *Lasiurus* cf. *seminolus*. The fossil differs from *Myotis* and agrees with the smaller species of *Lasiurus* in its larger size, elliptical humeral head oriented at a 45° angle to the shaft, and the reduced lesser tuberosity. The left humerus (V7204) referred to *Lasiurus* sp. by Weigel (1962:32) and later to *L. borealis* by Webb (1974:14) is a right humerus instead. I could not locate the left femur from Stratum 3 identified as *Lasiurus* sp. by Weigel.

Nycticeius humeralis (Rafinesque, 1818)

Referred material.—Stratum 2-V7228, nearly complete right mandible with m_2-m_3; V7211, nearly complete right humerus; Stratum 3-V7229, partial edentulous right mandible; V7209, complete right humer-

us; V7212, distal end of right humerus; V1603, complete left humerus; V7213-7216, V7231, proximal portions of left humeri; V7230, distal end of left humerus, V7217, one right and one left femur; Stratum unknown-V7208, nearly complete edentulous right mandible; V7210, complete right humerus; V7232, nearly complete left humerus; V7233, distal end of left humerus.

Recent distribution.—*Nycticeius humeralis* occurs throughout the eastern United States and along the Gulf Coast as far south as the state of Veracruz, Mexico. It is found throughout Florida and is one of the most common bats of south Florida (Jennings 1958), specimens having been taken as far south as Collier and Dade counties.

Fossil record.—The specimens of *N. humeralis* from Vero represent the first fossil record of the evening bat from Florida. The two specimens from Stratum 2 constitute the second record of *N. humeralis* from the Pleistocene of North America, the other occurrence being in Baker Bluff Cave in northeastern Tennessee (Guilday et al. 1978).

Description and comparisons,—The three mandibles referred to *N. humeralis* can be readily distinguished from *Myotis* and *Plecotus* by the presence of only two premolars, from *Pipistrellus* by their larger size, and from *Eptesicus*, *Eumops*, and *Lasiurus intermedius* by their considerably smaller size. The mandibles are generally similar in size to the two smaller species of *Lasiurus*, but they differ from them in possessing a longer, more slender mandibular ramus and a larger coronoid process, and in lacking a deep cleft between the paraconid and metaconid on all molars. The fossils can be differentiated from *Tadarida brasiliensis* by smaller size, presence of a single-rooted rather than a double-rooted P_3, strong rounded coronoid process, deep masseteric fossa, small entoconids on molars, and relatively large incisors (the incisors are small and compressed in *Tadarida*). The characters of these three mandibles, including size, length and depth of ramus, shape of coronoid process and masseteric fossa, and morphology of the dentition, agree closely with specimens of *N. humeralis* (see measurements in Table 1).

Twelve humeri from Vero are referable to *Nycticeius humeralis*. They can be separated readily from *Eptesicus* and *Eumops* by their smaller size, and from *Tadarida* and all species of *Lasiurus* by the hemispherical humeral head and reduced distal spinous process. Based on a number of characters, the humeri can easily be narrowed down to *Myotis*, *Pipistrellus*, and *Nycticeius*. The most reliable character on the proximal end of the humerus for separating the fossils from *Myotis* and *Pipistrellus* is the more prominent medial ridge extending ventrally from the lesser tuberosity and producing a larger fossa or concavity for the origin of the lateral head of the triceps muscle. In a posterior view of the proximal end, that portion of the humerus medial to the pectoral ridge

is wider in *Nycticeius* as a result of the better developed medial ridge. The distal half of the posterior surface of the humeral shaft is distinctly flattened in *Nycticeius* and the fossils, but is round in cross-section in the other two species. On the distal end of the humerus, the lateral edge of the articular surface (lateral epicondyle of the capitulum) extends lateral to the edge of the shaft in *Myotis* and *Pipistrellus*, but is in line with the shaft in the fossils and *Nycticeius*. *Nycticeius* and the fossils possess a prominent notch immediately proximal to the lateral edge of the capitulum that extends around the lateral edge almost to the anterior surface of the humeral shaft. This notch is not as well developed in the other two species. Finally, in *Nycticeius* there is a well developed, rounded tubercule on the lateral edge of the shaft just proximal to the notch, which is absent in *P. subflavus* and *M. austroriparius*. The region medial to the medial epicondyle (trochlea) is relatively large in *Myotis*, somewhat smaller in *Pipistrellus*, and very reduced in the fossils and *Nycticeius*. Therefore, although the humeri in these three species are superficially very similar, a number of characters can be used to separate them, and the fossils are clearly referable to *N. humeralis* (see measurements on humeri in Table 2).

Discussion.—Nycticeius humeralis is the most abundant fossil bat in the Vero site, with 17 identifiable elements representing a minimum of seven individuals. Evening bats roost primarily in buildings, hollow trees, and under the loose bark of trees. They seem to show a preference for cypress trees and are the common bat in Florida near cypress stands (Jennings 1958). Like the species of *Lasiurus*, *N. humeralis* is not known to enter caves, thus explaining the absence of this species from other Pleistocene sites in Florida that have produced bat fossils. Apparently, *N. humeralis* is not as subject to raptor predation as is *Lasiurus*, since species of the latter genus do on occasion appear in cave fossil deposits. Identification of fossil cypress, *Taxodium distichum*, from Stratum 3 (Berry 1917) supports Weigel's statement (1962:42) that there was a cypress pond in the vicinity of the Vero site. The presence of cypress trees and the preference of *Nycticeius humeralis* for roosting in cypress offer an explanation for the abundance of evening bat fossils at Vero.

Family Molossidae Gill

Tadarida brasiliensis (I. Geoffroy St. -Hilaire, 1824)

Referred material.—Stratum 3-V7219, proximal end of left humerus; Stratum unknown-V7218, nearly complete left mandible with m_2-m_3.

Recent distribution.—Tadarida brasiliensis is found primarily in the southern and western United States and then southward through Middle America, the West Indies, and much of South America. Brazil-

ian free-tailed bats occur throughout Florida, and according to Layne (1974) the species is the most successful bat in southern Florida, where it has been recorded as far south as Dade and Collier counties.

Fossil record.—*Tadarida brasiliensis* is known from three other fossil sites in eastern North America, two in Florida (Reddick IA and Nichol's Hammock) and the other in Mammoth Cave, Kentucky (outside the present range of the species). There are numerous Pleistocene records of *T. brasiliensis* from the southwestern United States and the West Indies.

Description and comparisons.—The mandible referred to *T. brasiliensis* is distinguishable from *Eumops* by its considerably smaller size and from *Pipistrellus* by its considerably larger size. The fossil differs from *Lasiurus*, *Eptesicus*, *Nycticeius*, *Myotis*, and *Plecotus* in the reduced coronoid process, shallow masseteric fossa, small compressed incisors, double-rooted p_3, and larger m_3 relative to m_2. *Myotis* and *Plecotus* both have the same number of premolar alveoli as *Tadarida*, but they possess single-rooted p_2 and p_3, while *Tadarida* lacks p_2 and has a double-rooted p_3. Based on the above combination of characters, the fossil mandible is readily identified as *T. brasiliensis* (see measurements, Table 1).

Although poorly preserved and lacking the lesser tuberosity, the proximal humerus here referred to *T. brasiliensis* is identifiable. Based on its small size and elliptical humeral head, the humerus can be distinguished from that of all Florida bats except the two small species of *Lasiurus* and *Tadarida*. The humerus is identified as *T. brasiliensis* by its broader and shorter pectoral ridge and greater distal extension of the medial ridge.

Discussion.—Only two fossils of *T. brasiliensis*, probably representing a single individual, have been identified from Vero. The Brazilian free-tailed bat is rare as a fossil in Florida, having been recorded from only three sites based on less than ten specimens. At the present time, *T. brasiliensis* in Florida roosts almost exclusively in man-made structures, such as in houses and under bridges (Jennings 1958). Although it has been observed in small numbers in several caves in Marion County, Florida (R. Franz, pers. comm.), these probably do not represent roosting colonies. In marked contrast to the southwest, where *T. brasiliensis* inhabits caves in colonies sometimes numbering into the millions, it is not known to roost in caves in the southeastern United States. Apparently, the warm humid atmosphere of Florida caves offers an unsuitable environment for roosting colonies (Jennings 1958). *Tadarida brasiliensis* in Florida has also been observed roosting under the dead fronds of palm trees in Lee and Charlotte counties in southwestern Florida, and in hollow mangrove trees in the Tampa Bay area (Jennings 1958). Palm

trees provide the natural roosting site for many species of Neotropical molossids, and it seems reasonable to hypothesize a similar roosting ecology for *T. brasiliensis* in Florida prior to the extensive construction of buildings. The probable tree-roosting habits of *T. brasiliensis*, coupled with their extremely rapid flight, would limit predation and help to explain their absence from most Florida fossil sites.

Eumops glaucinus floridanus (G. M. Allen, 1932)

Referred material.—Stratum 3-V7222, partial edentulous left mandible; V7224, proximal end of right radius; V7226, proximal end of left radius; V7227, one proximal and one distal end of femur; Stratum unknown-V7220, right maxilla with P^4-M^3; V7221, left mandible with p_3-m_3; V7223, proximal end of right humerus; V7225, proximal half of left radius.

Recent distribution.—*Eumops glaucinus* has the most restricted distribution of any bat in the United States, being known only from Charlotte and Dade counties in southernmost Florida. Wagner's mastiff bat also occurs in tropical America from southern Mexico south through Middle America, much of South America, and Cuba and Jamaica in the Greater Antilles. The species has a disjunct distribution, as it is not known to occur between southern Florida and southern Mexico.

Fossil record.—The fossil record of *E. glaucinus* is restricted to Florida, where it is known from Vero, Monkey Jungle Hammock (Martin 1977), and the late Pleistocene Melbourne fauna, Brevard County (Allen 1932; Ray et al. 1963). The fossil records from Brevard County and Indian River County (this paper) extend the known range of the species in Florida some 200 km north.

Descriptions and comparisons.—The cranial and postcranial elements here referred to *E. glaucinus* are from a very large bat, and thus need only be compared with the three largest species found in Florida—*E. glaucinus*, *Eptesicus fuscus*, and *Lasiurus intermedius*. A maxilla and partial rostrum agree with *E. glaucinus* and differ from *E. fuscus* and *L. intermedius* as follows: presence of a tiny peg-like P^3, stronger hypocone on M^1 and M^2, lack of a deeply incised nasal notch, vertical slit-like infraorbital foramen, and vertical orientation of rostrum dorsal to orbit, reflecting deep, laterally compressed snout (rostrum is dorsoventrally flattened in the two large vespertilionids). The mandible with p_3-m_3, can be differentiated from *E. fuscus* and *L. intermedius* as follows: presence of only two tiny incisors that are crowded between the canine and mandibular symphysis, double-rooted p_3, p_3 and p_4 subequal in size, and the posterior margins of trigonid and talonid on molars not at right angles to long axis of tooth row.

The proximal humerus referred to *E. glaucinus* can be readily distinguished from all other Florida bats by its very large size, teardrop-shaped humeral head oriented at a 45° angle to the shaft, short expanded pectoral ridge, and proximal extension of the greater tuberosity. The three radii are identified as *E. glaucinus* by the large, deep flexor fossa on the anterior surface just distal to the proximal articulation, the acutely triangular proximal end, and the strongly concave articular surface with a deep central groove for reception of the medial portion of the capitulum on the distal end of the humerus. The proximal and distal femur can be separated from all Florida vespertilionids by the small femoral head relative to the greater and lesser trochanters, relatively broader distal end, and more widely separated articular condyles. Among Florida bats, only *Tadarida brasiliensis* has femora with a similar morphology, but their small size eliminates them immediately.

Discussion.—Even though *Eumops glaucinus* is the second most abundant bat at Vero based on the total number of elements present (nine), a minimum of only two individuals is represented. The presence of *Eumops glaucinus* at Vero is of particular interest since this site is over 100 km north of the northernmost locality from which recent individuals of this species have been collected. A single fossil mandible of *E. glaucinus* is known from the Melbourne Site, located approximately 50 km north of Vero (Allen 1932; Ray et al. 1963). Until recently, living specimens of *E. glaucinus floridanus* had been collected only from man-made structures in the Miami area of Dade County in extreme southeastern Florida. Belwood (1981) discovered a small colony of *E. glaucinus* roosting in a hollow long-leaf pine, *Pinus palustris*, near Punta Gorda in Charlotte County on the southwest coast of Florida. Hollow trees appear to be the preferred natural roosting site of this species (Belwood 1981). The discovery of *E. glaucinus* in Charlotte County extends the modern range of the species in Florida 200 km westward and 100 km northward of Miami. With the addition of the three fossil records from Florida discussed above, the species is now known from three different localities in south Florida and two localities from the central portion of the state (Fig. 1).

Martin (1977) suggested that the presence of *Eumops glaucinus* in central Florida during the late Pleistocene represented a northward shift in winter isotherms indicative of tropical or subtropical conditions. Belwood's recent discovery of *E. glaucinus* in a part of Florida and in an ecological situation from which the species was previously unknown suggests that our knowledge of this bat is far from adequate. If *Eumops* did extend its range northward in response to warmer climates, why is it known in central Florida only from a late Wisconsinan site (Melbourne) in which climatic conditions were presumably drier and cooler than at

present, and a Holocene site (Vero) in which the climatic conditions were essentially similar to those at present? It would seem more likely that *Eumops* would have been found in one of the Sangamonian interglacial sites (Reddick, Haile, Arredondo, etc.), at a time during which climates were probably somewhat more tropical than they presently are.

As noted by Eger (1977) and Koopman (1971), the endemic Florida subspecies, *Eumops glaucinus floridanus*, is the most distinct form of the species. The Florida animal is characterized by its larger size, a feature also seen in the fossil representative of the species from Florida (see measurements in Table 3). According to Eger (1977), all Neotropical representatives of *E. glaucinus*, including those from the West Indies, are referable to the nominal subspecies, while only the Florida population is recognizable as a distinct subspecies. Baker and Genoways (1978) suggested the possibility that *E. glaucinus* invaded Florida from Cuba, a distance of only 200 km. However, the strong mainland Neotropical component of Florida's Pleistocene fauna, and the total lack of any other West Indian bats in the state, suggest strongly that the present distribution of *E. glaucinus* resulted from a warmer interglacial period when the Neotropical fauna was continuous around the Gulf Coast. Two other bats found in Florida during the late Pleistocene, *Desmodus stocki* and *Mormoops megalophylla*, also reflect this mainland Neotropical influence.

DISCUSSION

The fossil bat fauna from Vero is significant for several reasons. First, more species of bats (six) are represented at Vero than in any other fossil vertebrate fauna yet described from Florida. The two most diverse fossil chiropteran faunas from Florida listed by Webb (1974:14) were Reddick 1A, Marion County, with five species—*Desmodus stocki*, *Myotis austroriparius*, *Lasiurus borealis*, *L. intermedius*, and *Tadarida brasiliensis*—and Devil's Den, Levy County, with four species—*M. austroriparius*, *M. grisescens*, *Pipistrellus subflavus*, and *L. intermedius*. Second, among the ten or so Pleistocene and Holocene vertebrate faunas in Florida that contain abundant bat fossils, only the Vero deposit represents a depositional environment other than a cave, fissure, or sinkhole. The fossil deposits at Reddick consist of unconsolidated sediments filling caverns and solution pipes in the surrounding Eocene limestones. A cave-dwelling species, *Myotis austroriparius*, accounts for the great majority of bat remains at Reddick. The Devil's Den site is a water-filled sinkhole and cave system, presumably inhabited by the bats during a period of lower sea level and water tables in the late Wisconsinan and early Holocene. Cavernicolous bats also predominate at Devil's Den. In fact, all of the major North American Pleistocene sites listed by Kurtén and Anderson (1980) that contain large bat faunas were deposited in caves and are dominated by cave-inhabiting species.

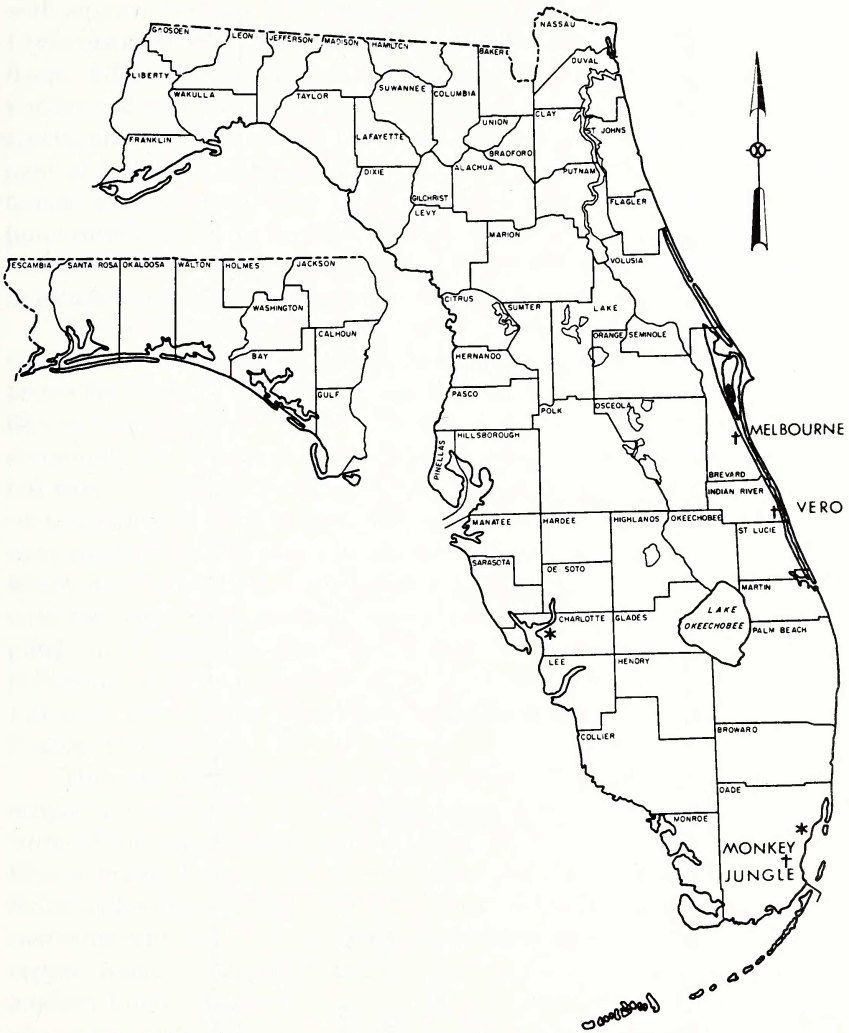

Fig. 1. Pleistocene and Recent occurrences of *Eumops glaucinus floridanus* in Florida. Asterisks (*) indicate Recent records, daggers (†) and name of fauna indicate Pleistocene records.

Based on studies of the sediments, fossil plants, and fossil vertebrates, Weigel (1962) concluded that the fossil deposits at Vero represented a pond or marsh habitat. Berry (1917) studied the fossil plants from Stratum 3 at Vero. Among the more informative plants he identified were cypress, *Taxodium distichum*, and three species of obligate pond inhabitants: water lettuce, *Pistia*; pond apple, *Anona glabra*; and water shield, *Brasenia purpurea*. A number of the other fossil plants from Vero also have aquatic tendencies. According to Weigel (1962), almost 50% of the vertebrates from Strata 2 and 3 are forms associated

Table 3. Comparison of cranial and mandibular measurements of fossil *Eumops glaucinus* from Vero with Recent *E. glaucinus* from Florida.[1]

	alveolar length of maxillary tooth row	length of M^1-M^3	length of M^1	width of M^1	length of M^2	width of M^2	depth of ramus below m_2	length of m_1	width of m_1	length of m_2	width of m_2
Eumops glaucinus											
Recent	$10.0 \pm \frac{0.2}{7}$	$6.2 \pm \frac{0.1}{7}$	$2.6 \pm \frac{0.1}{7}$	$3.4 \pm \frac{0.1}{7}$	$2.5 \pm \frac{0.1}{7}$	$3.4 \pm \frac{0.1}{7}$	$2.8 \pm \frac{0.4}{7}$	$2.7 \pm \frac{0.1}{7}$	$1.8 \pm \frac{0.1}{7}$	$2.7 \pm \frac{0.1}{7}$	$1.7 \pm \frac{0.1}{7}$
	(9.6-10.3)	(6.1-6.4)	(2.5-2.6)	(3.2-3.5)	(2.4-2.6)	(3.2-3.6)	(2.3-3.2)	(2.6-2.8)	(1.7-1.8)	(2.6-2.7)	(1.7-1.8)
Fossil											
V7220	10.1	6.3	2.6	3.5	2.4	3.5					
V7221							3.1	2.7	1.8	2.7	1.7

[1] Mean, standard deviation, sample size, and observed range (in parentheses), respectively, are given for Recent specimens.

with aquatic habitats, including such obligate freshwater species as gar, *Lepisosteus*; bowfin, *Amia*; *Siren* and *Amphiuma*; two species of ranid frogs; *Alligator*; two species of water snake, *Nerodia*; four species of kinosternid mud turtles; a number of species of ducks, rails, herons, and egrets; and the round-tailed muskrat, *Neofiber alleni*. The large component of aquatic vertebrates supports the sedimentological and paleobotanical evidence that the deposits were formed in a shallow freshwater pond or marsh. Based on the presence of a number of strictly terrestrial forms in the fauna, several other habitats were certainly present in the immediate vicinity, including mesic hammock and pine flatwoods.

The presence of a diverse bat fauna at Vero is somewhat difficult to explain in the context of the freshwater pond or marsh habitat suggested by Weigel (1962). In Weigel's scenario of Vero (1962:49), "Bats flew over the pond and marsh in search of insects. . . ." It is true that bats commonly fly over open water, both in search of insects and to drink, but bats are usually absent or extremely rare in fossil deposits sampling such habitats. A large number of Pleistocene sites in peninsular Florida were deposited in marshes, swamps, or fluvial environments, several of which have abundant microvertebrate samples. Yet, except for Vero, only two specimens of fossil bats are known from Florida sites sampling such habitats—the type specimen of *Molossides floridanus* (=*Eumops glaucinus floridanus*) from Melbourne, and a mandible of *Lasiurus intermedius* from the Glyptodont Site, Catalina Gardens, Pinellas County.

The roosting ecology of the bats recorded from Vero provides some insight into the problem, as all six species are known to roost in trees. None of the bats from Vero normally roost in caves in the southeastern United States. In contrast, the two most abundant and widespread bats found as fossils in northern Florida cave and fissure deposits are *Myotis austroriparius* and *Pipistrellus subflavus*, both of which roost in caves at certain times of the year. The absence of these two species from the modern fauna of south Florida, except for accidental occurrences, is almost certainly related to the absence of dry caves south of Citrus and Marion counties.

Unlike any other Quaternary bat fauna known from Florida, Vero offers a unique view of the late Pleistocene and Holocene bat fauna associated with riparian habitats. Generally, tree-roosting bats and bats associated with freshwater habitats are rare or totally absent from fossil sites deposited in caves, fissures, or sinkholes in north Florida, as in the case of *Nycticeius humeralis* and *Eumops glaucinus*. The exact mode of deposition of the bat fossils at Vero is still a matter of speculation. Perhaps the bat carcasses accumulated in hollow trees alongside the pond or marsh and were eventually washed in when the trees fell. The great abundance of other small mammals in the Vero deposit, especially shrews and small rodents, suggests the possibility of a raptor roost in the vicinity of the pond, most likely that of *Tyto alba*.

Layne (1974) recorded seven bat species from Florida south of Lake Okeechobee. Although Vero is slightly north of this area, it is located in the southern half of the Florida peninsula. Among these seven species, *Myotis austroriparius* and *Pipistrellus subflavus* almost certainly do not breed in south Florida, and Layne considered their occurrence in the region to be accidental. The remaining five species comprise the native chiropteran fauna of south Florida: *Lasiurus seminolus*, *L. intermedius*, *Nycticeius humeralis*, *Tadarida brasiliensis*, and *Eumops glaucinus*—all of which are known from Vero. All six species of bats from Vero, including *Eptesicus fuscus*, might be expected to occur in that vicinity at the present time, with the possible exception of *Eumops glaucinus*. Apparently, the chiropteran fauna of south Florida had become established by the early Holocene and has remained essentially unchanged to the present time.

ACKNOWLEDGMENTS.— I thank R. Franz, A. E. Pratt, and K. T. Wilkins for their helpful comments on an earlier draft of this manuscript. L. Wilkins and C. A. Woods allowed me access to the Florida State Museum Recent mammal collections. Shaen Williams typed the final draft of the paper. This is Univeristy of Florida Contribution to Vertebrate Paleontology No. 225.

LITERATURE CITED

Allen, Glover M. 1932. A Pleistocene bat from Florida. J. Mammal. *13*:256-259.

Baker, Robert J., and H. H. Genoways. 1978. Zoogeography of Antillean bats. Pp. 53-97 *in* F. B. Gill (Ed.). Zoogeography in the Caribbean. Spec. Publ. Acad. Nat Sci. Phila. *13*:1-128.

Barbour, Roger W., and W. H. Davis. 1969. Bats of America. Univ. Presses Kentucky, Lexington. 286 pp.

Belwood, J. J. 1981. Wagner's mastiff bat, *Eumops glaucinus floridanus*, (Molossidae) in southwestern Florida. J. Mammal. *62*:411-413.

Berry, Edward W. 1917. The fossil plants from Vero, Florida. J. Geol. *25*:661-666.

Eger, Judith L. 1977. Systematics of the genus *Eumops* (Chiroptera:Molossidae). Royal Ont. Mus. Life Sci. Contrib. *110*:1-69.

Guilday, John E., H. W. Hamilton, E. Anderson and P. W. Parmalee. 1978. The Baker Bluff cave deposit, Tennessee, and the late Pleistocene faunal gradient. Bull. Carnegie Mus. Nat. Hist. *11*:1-67.

Hirschfeld, Sue E. 1968. Vertebrate fauna of Nichol's Hammock, a natural trap. Q. J. Fla. Acad. Sci. *31*:177-189.

Jennings, William L. 1958. The ecological distribution of bats in Florida. Unpubl. Ph.D. dissert., Univ. Florida, Gainesville. 126 pp.

Koopman, Karl F. 1971. The systematic and historical status of the Florida *Eumops* (Chiroptera, Molossidae). Am. Mus. Novit. *2478*:1-6.

Kurtén, Björn, and E. Anderson. 1980. Pleistocene Mammals of North America. Columbia Univ. Press, New York. 442 pp.

Lawrence, Barbara. 1943. Miocene bat remains from Florida, with notes on the generic characters of the humerus of bats. J. Mammal. *24*:356-369.

Layne, James N. 1974. The land mammals of South Florida. Pp. 386-413 *in* P. J. Gleason (Ed.). Environments of South Florida: Present and Past. Miami Geol. Soc. Mem. *2*:1-452.

Martin, Robert A. 1972. Synopsis of late Pliocene and Pleistocene bats of North America and the Antilles. Am. Midl. Nat. *87*:326-335.

_____ . 1977. Late Pleistocene *Eumops* from Florida. Bull. New Jersey Acad. Sci. *22*:18-19.

_____ , and S. D. Webb. 1974. Late Pleistocene mammals from the Devil's Den fauna, Levy County. Pp 114-145 *in* S. D. Webb (Ed.). Pleistocene Mammals of Florida. Univ. Presses Florida, Gainesville. 270 pp.

Meltzer, David J., and J. I. Mead. 1983. The timing of late Pleistocene extinctions in North America. Quat. Res. (NY) *19*:130-135.

Miller, Gerrit S., Jr. 1907. The families and genera of bats. U.S. Nat. Mus. Bull. *57*:1-282.

Ray, Clayton E. 1957. A list, bibliography, and index of the fossil vertebrates of Florida. Fla. Geol. Surv. Spec. Publ. *3*:1-175.

_____ , S. J. Olsen and H. J. Gut. 1963. Three mammals new to the Pleistocene fauna of Florida, and a reconsideration of five earlier records. J. Mammal. *44*:373-395.

Sellards, E. H. 1916. Human remains and associated fossils from the Pleistocene of Florida. Fla. Geol. Surv. 8th Annu. Rep. pp. 122-160.

_____ . 1917. On the association of human remains and extinct vertebrates at Vero, Florida. J. Geol. *25*:4-24.

Smith, James D. 1972. Systematics of the chiropteran family Mormoopidae. Univ. Kans. Mus. Nat. Hist. Misc. Publ. *56*:1-132.

Szalay, Frederick S. 1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bull. Am. Mus. Nat. Hist. *140*:193-330.

Vaughan, Terry A. 1959. Functional morphology of three bats: *Eumops*, *Myotis*, and *Macrotus*. Univ. Kans. Publ. Mus. Nat. Hist. *12*(1):1-153.

Webb, S. David. 1974. Chronology of Florida Pleistocene mammals. Pp. 5-31 *in* S. D. Webb (Ed.). Pleistocene Mammals of Florida. Univ. Presses Florida, Gainesville. 270 pp.

Weigel, Robert D. 1962. Fossil vertebrates of Vero, Florida. Fla. Geol. Surv. Spec. Publ. *10*:1-59.

Accepted 27 May 1984